

## A new theoretical approach for the study of monophyly of the Brachyura (Crustacea: Decapoda) and its impact on the Anomura

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### Abstract

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The primitive crabs consist of the Cyclodorippidae Ortmann, 1892; Cymonomidae Bouvier, 1897; Dromiidae de Haan, 1833; Dynomenidae Ortmann, 1892; Homolodromiidae Alcock, 1900; Homolidae de Haan, 1839; Latreilliidae Stimpson, 1858; Phyllotymolinidae Tavares, 1998; Poupiniidae Guinot, 1991; and Raninidae de Haan, 1841. The primitive crabs were transferred for the first time from the Brachyura to the Anomura by H. Milne Edwards (1832). Since then, they have been moved, individually or collectively, from the Anomura to the Brachyura and vice-versa with each successive revision. The high classification of both, Anomura and Brachyura, will not attain stability until the systematic position of the primitive crabs is established on a firm basis. The question of whether the Podotremata, in whole or in part, belongs or not to the Brachyura is discussed herein from a cladistic perspective. The argument is made that there are four different assumptions hidden within this question, and that only when they are explicitly considered will real progress be made towards a better understanding of brachyuran interrelationships.

### Keywords

Crustacea, Brachyura, Podotremata, Anomura, Dromiidae, Dynomenidae, Homolodromiidae, Homolidae, Latreilliidae, Poupiniidae, Cyclodorippidae, Cymonomidae, Phyllotymolinidae, Raninidae, cladistics, phylogeny, classification

### Introduction

Whether the Brachyura (Podotremata Guinot, 1977 + Heterotremata Guinot, 1977 + Thoracotremata Guinot, 1977) are monophyletic or not has long been disputed by decapodologists. Efforts to address the question of brachyuran monophyly include the analysis of larval features (e.g. Williamson, 1976; Williamson and Rice, 1996; Rice, 1980; 1981a; 1981b; 1983; Martin, 1991; McLay et al., 2001); the fossil record (e.g. Glaessner, 1969: 439; Schram and Mapes, 1984; Guinot, 1993; Bishop et al., 1998; Guinot and Tavares, 2001); eye structure and optics (e.g. Fincham, 1980; 1984; 1988; Gaten, 1998); spermatozoa ultrastructure (Jamieson, 1990; 1994; Jamieson et al., 1995; Guinot et al., 1994; 1998); and molecular techniques (e.g. Spears et al., 1992).

Questions related to the monophyly of the Brachyura are examined here from a cladistic perspective. One persistent problem is whether the Podotremata, or part thereof, belongs to the Brachyura or not. The primitive crabs were formally placed in the Brachyura by Latreille (1802) (see Guinot and Tavares, in press). Because primitive crabs share with Anomura the female gonopore on the coxa of the third pereopod, and their

abdomen and abdominal appendages also share overall similarities, H. Milne Edwards (1832) argued that they should be transferred from Brachyura to Anomura. Since then, the primitive crabs have been moved to the Anomura or retained in the Brachyura with each successive revision. A number of taxonomic schemes have been proposed accordingly: e.g. Anomura Pterygura (true anomurans) versus Anomura Apterura (primitive crabs) (H. Milne Edwards, 1837); Brachyura Anomala (primitive crabs) versus Brachyura genuina (true crabs) (Alcock, 1899; Stebbing, 1910); Podotremata (primitive crabs) versus Eubrachyura (true crabs, Heterotramata + Thoracotremata) (Guinot, 1977; de Saint Laurent, 1980). Although Guinot's classification has attained broad acceptance, the lack of a general consensus on the systematic position of the primitive crabs has generated substantial instability in the classification (e.g. Bowman and Abele, 1982; Martin and Davis, 2001). The systematic position of the primitive crabs is a major concern in decapodology, and the higher classification of both Anomura and Brachyura cannot be stable while their position remains unsettled.

The question of whether the Podotremata, or part of it, belongs or not to the Brachyura is investigated here from a

cladistic perspective. Four points are hidden within this issue. In the way it has been previously formulated, an objective answer to the question "Do the Podotremata, or part of it, belongs to the Brachyura" cannot be provided. It must be noted that the answer entirely depends upon the concept that one wishes to apply to the Brachyura. Rice (1980: 289) implied as much when he mentioned that "The position of the more primitive crab-like groups was a particularly contentious problem during the last century when . . . the dromiids, homolids and raninids individually or collectively, seemed to move in or out of the Brachyura with each successive revision". It is worth noting that the question of whether the Brachyura is monophyletic traditionally appears in terms of groups that should move in or out. When the problem is approached simply in terms of "in or out", the answer cannot be but largely subjective. Subjectivity arises when one wishes to understand how two groups (e.g. primitive crabs versus true crabs) are related to each other: taken alone two groups will always be related to each other at some level (Fig. 1). Therefore, lumping or splitting is largely a subjective decision. In other words, lumping or splitting depends on the level of generality (Nelson, 1978; Wiley, 1981: 126) of the character(s) selected to define the group.

In the case of Brachyura, the assemblage Heterotremata + Thoracotremata (= Eubrachyura de Saint Laurent, 1980) is defined by at least two unambiguous synapomorphies, namely the female sexual opening (vulva) on sternite 6 (Hartnoll, 1968; Guinot, 1977; 1979; Tavares and Secretan, 1993), and the presence of a sella turcica (Audouin and Milne Edwards, 1827; H. Milne Edwards, 1851; Bourne, 1922; Gordon, 1963; Secretan, 1998). If the sternal position of the female sexual opening, and the sella turcica are used to delimit the Brachyura, the Podotremata should be removed. However, use of a more generalised synapomorphy renders possible inclusion of Podotremata, or part, in the Brachyura. Indeed, since H. Milne Edwards (1832), parts or all of what is now the Podotremata have frequently been transferred (to the Anomura) or left in the Brachyura according to the level of generality of the characters that have been chosen. The study by Spears et al. (1992: 446) typically illustrated this situation. They obtained results from sequence-divergence estimates and phylogenies inferred by maximum parsimony analyses of aligned nucleotide sequences, which "suggest that (1) the Raninidae demarcate the lower limit of the Brachyura, and form a distinct lineage that diverged early from the lineage leading to other members of this infraorder, as indicated by a number of autapomorphic characters in the 18S rRNA molecule; and (2) the Dromiidae should be removed from the Brachyura...". From Spears et al.'s (1992) results it follows that there are three possible solutions to "demarcate the lower limit of the Brachyura": (1) set the lower limit at the base of the branch that unites the Heterotremata with the Thoracotremata; (2) set the lower limit, as Spears et al. (1992) did, at the base of the branch that unites the Raninidae with the group (Heterotremata + Thoracotremata); and (3) set the lower limit at the base of the branch that unites part of the Dromiidae with the group Raninidae + (Heterotremata + Thoracotremata). All solutions are equivalent but which one is to be retained depends entirely upon the level of generality of the character(s)

chosen to demarcate the Brachyura. Williamson and Rice (1996: 285) implicitly expressed a similar opinion: "Spears et al. (1992) interpreted their molecular data as 'clearly' excluding the dromiids from the Brachyura, but the definition of this group is somewhat arbitrary whether based on morphological or molecular data. Under a slightly wider definition, the rRNA data may be interpreted as supporting the inclusion of *Dromia*, but not *Hypoconcha*, in the Brachyura."

In addition to difficulties inherent to the monophyly of the Brachyura, one should consider the framework implicit in the way the problem is posed. From a cladistic perspective, and depending on the existence or not of evidence for a monophyletic Brachyura (Podotremata + Heterotremata + Thoracotremata), and/or a monophyletic Podotremata, there are four assumptions in the traditional discussion. These assumptions have so far not been clearly formulated because they have been confused by the question "Do the Podotremata or part of it belong in the brachyurans" (Tavares, 1993).

Only when those four assumptions are explicitly taken into consideration will progress be made towards a better understanding of brachyuran interrelationships. While new answers are not provided herein, it is believed that new questions are necessary to shed new light on the problem. All four assumptions consider that both Heterotremata + Thoracotremata and the Decapoda are monophyletic (Burkenroad, 1981; Guinot, 1979; Guinot and Tavares, 2001; Schram, 2001).

*Assumption 1:* The Brachyura (Podotremata + Heterotremata + Thoracotremata) is monophyletic as is the subclade Podotremata (Fig. 2). The corollary of this assumption is that the Podotremata is the sister group of Heterotremata + Thoracotremata group. This means that under assumption 1 there is no issue of which podotreme family is most closely related to the Heterotremata + Thoracotremata clade. This contrasts dramatically with trends in the literature concerned with establishing the lower limit of the brachyurans.

Scholtz and Richter (1995) proposed seven synapomorphies of the Brachyura. Guinot and Tavares (2001) suggested that the double spermatheca (sensu Tavares and Secretan, 1993) constitutes a synapomorphy shared by all Podotremata and not found in any other Decapoda so far. From the above perspective, it becomes clear that to concentrate on whether such characters can really be interpreted as synapomorphies appears more reasonable than to raise questions, a priori, about the lower level of the brachyurans.

*Assumption 2:* The Brachyura (Podotremata + Heterotremata + Thoracotremata) is monophyletic; the Podotremata is para- or polyphyletic (Fig. 3).

The corollary to this assumption is that at least one of the ten families currently included in the Podotremata is more closely related to the Heterotremata + Thoracotremata group than to the remaining families of Podotremata. Should such be the case it then becomes relevant to search for the group of podotrematous crabs that is the sister taxon of the eubrachyurans (Heterotremata + Thoracotremata). The search for the "lower limit" of the Brachyura only becomes necessary if the "lower limit" is interpreted to be the most basal branch of the brachyuran clade.

*Assumption 3:* The Brachyura (Podotremata +

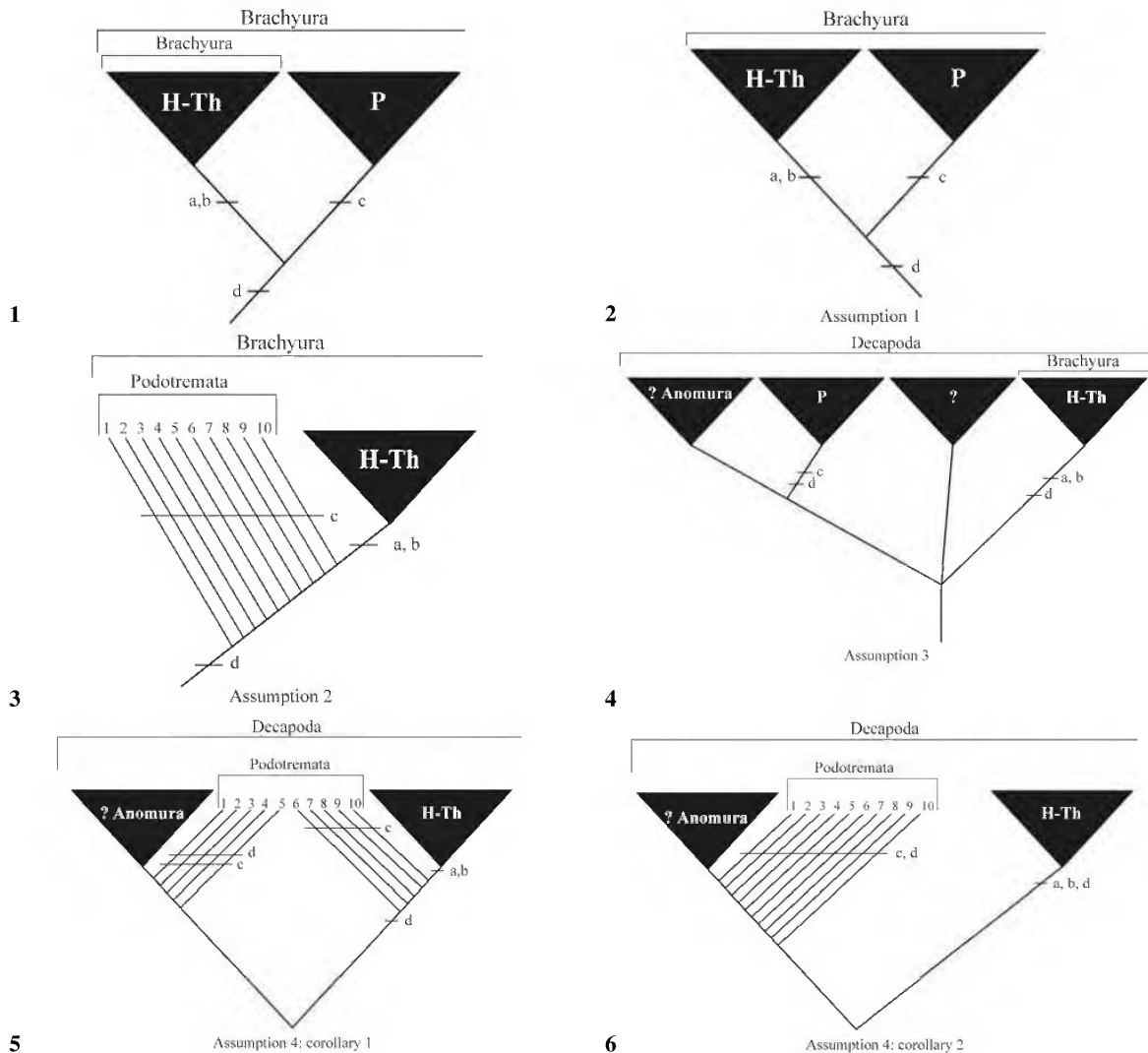


Figure 1. Synapomorphy “d” supports the inclusion of the Podotremata (P) in the Brachyura, while the use of less generalized synapomorphies (a, b) in the definition will result in the exclusion of the Podotremata from the Brachyura. Synapomorphies: a, female sexual opening on thoracic sternite 6; b, presence of sella turcica; c, paired spermatheca; d, intertagmal phragma fused with thoracic interosternite 8/7 (pers. obs.). Other abbreviations: H, Heterotremata; Th, Thoracotremata.

Figure 2. Assumption 1: both the Brachyura (H + Th + P) and Podotremata (P) are monophyletic. Under assumption 1 it makes no sense to search for the “lower limit” of the Brachyura. Synapomorphies and abbreviations as in Fig. 1.

Figure 3. Assumption 2: Brachyura (H + Th + P) monophyletic; Podotremata (P) not monophyletic. Under assumption 2 it becomes meaningful to search for the sister taxa of the Heterotremata + Thoracotremata clade. Synapomorphies and abbreviations as in Fig. 1.

Figure 4. Assumption 3: Brachyura (H + Th + P) not monophyletic; Podotremata (P) monophyletic. Under assumption 3 searching for the “lower limit” of the Brachyura among the Podotremata makes no sense. Synapomorphies and abbreviations as in Fig. 1.

Figure 5. Assumption 4: both Brachyura (H + Th + P) and Podotremata (P) not monophyletic. According to corollary 1 searching for the sister taxa of the Heterotremata + Thoracotremata clade and searching for the most basal branch of the brachyuran clade becomes truly relevant. Note that one set of the Podotremata is positioned as paraphyletic complex closely related to the Heterotremata + Thoracotremata clade (H-Th). Synapomorphies and abbreviations as in Fig. 1.

Figure 6. Assumption 4; corollary 2. Searching for the most basal branch of the brachyuran clade (“the lower limit”) among the Podotremata is completely meaningless. Note that none of the Podotremata (P) is closely related to the Heterotremata + Thoracotremata clade; all form a paraphyletic complex more closely related to some other group of decapods. Synapomorphies and abbreviations as in Fig. 1.

Heterotremata + Thoracotremata) are not monophyletic; the clade Podotremata is monophyletic (Fig. 4). The corollary to this assumption is that the Podotremata is more closely related to some other group of decapods (e.g. Anomura), than to the Heterotremata + Thoracotremata clade. This means that the name Brachyura would include only the group Heterotremata + Thoracotremata. Under this assumption, searching for the lower limit of the Brachyura among the podotrematous crabs makes no sense.

**Assumption 4:** The Brachyura (Podotremata + Heterotremata + Thoracotremata) is not monophyletic; the Podotremata is not monophyletic (Fig. 5). This assumption has two corollaries, as far as the Podotremata is concerned. First, one paraphyletic set of the ten families of Podotremata may be more closely related to the Heterotremata + Thoracotremata, with the rest of the families forming another assemblage more closely related to some other group of decapods (e.g. Anomura). The Brachyura should then consist of the Heterotremata + Thoracotremata + the related set of podotrematous crabs (e.g. families 5–9; Fig. 5). In this case, the search for the sister taxon of the Heterotremata + Thoracotremata group, and the search for the most basal branch of the brachyuran clade, becomes relevant.

Second corollary, none of the Podotremata is closely related to the Heterotremata + Thoracotremata group. This means that all Podotremata are a paraphyletic complex closely related to some other group of decapods (e.g. Anomura) (Fig. 6). The term Brachyura would then apply only to the Heterotremata + Thoracotremata group, and a search for the most basal branch of the brachyuran clade, “the lower limit” among the Podotremata, is meaningless.

## Conclusions

It is worth noting the central role played by the concept of monophyly of the Podotremata.

If the monophyletic status of the Podotremata cannot be demonstrated, then it is likely that: (1) at least one family or any monophyletic assemblage (of nine families at most, out of the ten existing families of Podotremata) is related to the Heterotremata + Thoracotremata clade; and (2) the podotreme families are more closely related to some other group of decapods (likely the Anomura) than to the Heterotremata + Thoracotremata.

On the other hand, if the monophyly of the Podotremata is confirmed it is not possible to have only part of the Podotremata closely related to the Heterotremata + Thoracotremata. In that case, all members of the Podotremata are equally related to the Heterotremata + Thoracotremata clade or none of them are, and searching for the lower limit of the brachyurans among the Podotremata is meaningless. In another words, a priori questions about “the lower limit of the Brachyura” compromises a far more important and central question, which is the monophyletic status of the Podotremata. The “lower limit” issue (the most basal branch of the brachyuran clade) only becomes truly relevant if the monophyletic status of the Podotremata cannot be demonstrated.

The inclusion of both, the primitive crabs and the

Thalassinidea (since Borradaile, 1903) in the Anomura resulted in two major obstacles to the stability of higher anomuran classification. Currently, there is little doubt that the Thalassinidea should be set apart from the anomurans (Scholtz and Richter, 1995; McLaughlin and Lemaitre, 1997; Tudge, 1997), and thus, their unlikely return no longer threatens the stability of the higher classification of anomurans. In contrast, the lingering uncertainties about the systematic position of the primitive crabs is a permanent threat to the stability of the higher classification of both Anomura and Brachyura. It is apparent that this situation has affected anomuran classification less than brachyuran classification, even though the Anomura is a much smaller group. It is a fortune that students of decapod phylogeny have refrained from rushing into new taxonomic schemes for the Anomura until a more clear outline of the decapod tree history emerges.

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## References

- Alcock, A. 1899. *An account of the deep-sea Brachyura collected by the Royal Indian Marine Survey Ship "Investigator"*. Trustees of the Indian Museum: Calcutta. 85 pp.
- Audouin, V., and Milne Edwards, H. 1827. Recherches anatomiques et physiologiques sur la circulation des Crustacés. *Annales des Sciences naturelles (Zoologie)* 11: 283–314; 352–393.
- Bishop, G.A., Feldmann, R.M., and Vega, F. 1998. The Dakoticantridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico. *Contributions to Zoology* 67(4): 237–255.
- Bourne, G.C. 1922. The Raninidae: a study in carcinology. *Journal of the Linnean Society (Zoology)* 35: 25–79.
- Bowman, T. E., and Abele L. G. 1982. Classification of the Recent Crustacea. Pp. 1–27 in: Abele, L. G. (ed), *The biology of Crustacea. Vol. 1. Systematics, the fossil record, and biogeography*. Academic Press: New York.
- Burkenroad, M. D. 1981. The higher taxonomy and evolution of Decapoda (Crustacea). *Transactions of the San Diego Society of Natural History*, 19(17): 251–268.
- Fincham, A.A. 1980. Eyes and the classification of the malacostracan crustaceans. *Nature* 287(5784): 729–731.
- Fincham, A.A. 1984. Ontogeny and optics of the eyes of the common prawn *Palaemon (Palaemon) serratus* (Pennant, 1777). *Zoological Journal of the Linnean Society* 81: 89–113.
- Fincham, A.A. 1988. Ontogeny of anomuran eyes. *Symposium of the Zoological Society of London* 59: 123–155.
- Gaten, E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contributions to Zoology* 67(4): 223–235.

- Glaessner, M.F. 1969. Decapoda. Pp. R399–R651 in: Moore, R.C. (ed.), *Treatise on invertebrate paleontology, Part R, Arthropoda 4*. Vol. 2. Geological Society of America and University of Kansas Press.
- Gordon, I. 1963. On the relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura. Pp. 51–57 in: Whittington, H.B., and Rolfé, W.D.I. (eds), *Phylogeny and evolution of Crustacea*. Special Publication Museum of Comparative Zoology: Cambridge.
- Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés, Décapodes, Brachyours. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Paris* (D) 285: 1049–1052.
- Guinot, D. 1979. Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. *Mémoires du Muséum national d'Histoire naturelle* (A) 112: 1–354.
- Guinot, D. 1993. Données nouvelles sur les crabes primitifs (Crustacea Decapoda Brachyura Podotremata). *Comptes Rendus de l'Académie des Sciences, Paris* 316: 1225–1232.
- Guinot D., Jamieson, B.G.M., and Richer de Forges, B. 1994. Relationship of Homolidae and Dromiidae: evidence from spermatozoal ultrastructure (Crustacea, Decapoda). *Acta Zoologica* 75: 255–267.
- Guinot D., Jamieson, B.G.M., Richer de Forges, B., and Tudge, C.C. 1998. Comparative spermatozoal ultrastructure of the three dromiacean families exemplified by *Homolodromia kai* (Homolodromiidae), *Sphaerodromia lamellata* (Dromiidae), and *Dynomene tanensis* (Dynomeniidae) (Podotremata: Brachyura). *Journal of Crustacean Biology* 18(1): 78–94.
- Guinot, D., and Tavares, M. 2001. Une nouvelle famille de crabes du Crétacé, et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema* 23(3): 507–546.
- Guinot, D., and Tavares, M. (in press). The subfamilies of the Dromiidae de Haan, 1833, with new diagnoses and description of new genera and species (Crustacea, Decapoda, Brachyura). *Zoosystema*.
- Hartnoll, R.G. 1968. Morphology of the genital ducts in female crabs. *Journal of the Linnean Society (Zoology)* 47(312): 279–300.
- Jamieson, B.G.M. 1990. Ultrastructure and phylogeny of crustacean spermatozoa. *Memoirs of the Queensland Museum* 31: 109–142.
- Jamieson, B.G.M. 1994. Phylogeny of the Brachyura with particular reference to the Podotremata: evidence from a review of spermatozoal structure (Crustacea, Decapoda). *Philosophical Transactions of the Royal Society of London* (B) 345(1314): 335–465.
- Jamieson, B.G.M., Guinot, D., and Richer de Forges, B. 1995. Phylogeny of the Brachyura (Crustacea: Decapoda): evidence from spermatozoal structure. *Mémoires du Muséum national d'Histoire naturelle, Paris* 166: 265–283.
- Martin, J.W. 1991. Crabs of the family Homolodromiidae, III. First record of the larvae. *Journal of Crustacean Biology* 11(1): 156–161.
- Martin, J.W., and Davis, G.E. 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series* 39: 1–124.
- McLaughlin, P. A., and Lemaitre, R. 1997. Carcinization in the Anomura – fact or fiction? I. Evidence from adult morphology. *Contributions to Zoology* 67(2): 79–123.
- McLay, C.L., Lim, S.S.L., and Ng, P.K.L. 2001. On the first zoea of *Lauridromia indica* (Gray, 1831), with an appraisal of the generic classification of the Dromiidae (Decapoda: Brachyura) using larval characters. *Journal of Crustacean Biology* 21(3): 733–747.
- Milne Edwards, H. 1834–1837. *Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux*. Librairie Encyclopédique de Roret: Paris. 468 pp.
- Milne Edwards, H. 1851. *Observations sur le squelette tégumentaire des Crustacés Décapodes, et sur la morphologie de ces animaux*. *Annales des Sciences naturelles (Zoologie)*, (sér. 3) 16: 221–291.
- Nelson, G. 1978. Ontogeny, phylogeny, and the biogenetic law. *Systematic Zoology* 27: 324–345.
- Rice, A.L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* 35(3): 271–424.
- Rice, A.L. 1981a. The megalopa in brachyuran crabs. The Podotremata Guinot. *Journal of Natural History* 15: 1003–1011.
- Rice, A.L. 1981b. Crab zoeae and brachyuran classification: a reappraisal. *Bulletin of the British Museum of natural History (Zoology)* 40(5): 287–296.
- Rice, A.L. 1983. Zoeal evidence for brachyuran phylogeny. *Crustacean Issues* 1: 313–339.
- Saint Laurent, M. de, 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. II. Heterotremata et Thoracotremata Guinot, 1977. *Comptes Rendus de l'Académie des Sciences de Paris* 290: 1317–1320.
- Scholtz, G., and Richter, S., 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society* 113: 289–328.
- Schram, F. 2001. Phylogeny of decapods: moving towards a consensus. *Hydrobiologia* 449: 1–20.
- Schram, F., and Mapes, R.H. 1984. *Imocaris tuberculata*, n. gen., n. sp. (Crustacea: Decapoda) from the Upper Mississippian Imo Formation, Arkansas. *Transactions of the San Diego Society of Natural History* 20: 165–168.
- Secretan, S. 1998. The sella turcica and the endophragmal system of decapods. *Journal of Natural History* 32: 1753–1767.
- Spears, T., Abele, L.G., and Kim, W. 1992. The monophyly of brachyuran crabs: a phylogenetic study based on 18S rRNA. *Systematic Biology* 41(4): 446–461.
- Stebbing, T. R. R. 1910. General catalogue of South African Crustacea. (Part V of S.A. Crustacea, for the Marine Investigations in South Africa). *Annals of the South African Museum* 6: 281–593.
- Tavares, M. 1993. Cladistic insights into the monophyly of the Brachyura. Pp. 65–66 in: *International Senckenberg Symposium Crustacea Decapoda*, October 18–22. Abstract volume. Senckenberg Museum: Frankfurt a.M.
- Tavares, M., and Secretan, S. 1993. La notion de thelycum et de spermatheque chez les Crustacés Décapodes. *Comptes Rendus de l'Académie des Sciences, Paris* 316(III): 133–138.
- Tudge, C. C. 1997. Phylogeny of the Anomura (Decapoda: Crustacea): spermatozoa and spermatophore morphological evidence. *Contributions to Zoology* 67(2): 125–141.
- Wiley, E.O. 1981. *Phylogenetics. The theory and practice of phylogenetic systematics*. John Wiley and Sons: New York. 439 pp.
- Williamson, D.I. 1976. Larval characters and the origin of crabs. *Thalassia Jugoslavica* 10: 401–414.
- Williamson, D.I., and Rice, A.L. 1996. Larval evolution in the Crustacea. *Crustaceana* 69(3): 267–289.